

No. 2.—*The Lower Permian Insects of Kansas. Part I.*

*Introduction and the Order Mecoptera*

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INTRODUCTION

THE Permian has long been recognized as the period of most rapid evolution of the insects. The contrast between the archaic fauna of the Upper Carboniferous and the relatively modern one of the Triassic is fully as great as that between the faunas of the Triassic and the Recent. Until lately, however, the fossil record of the Permian has been nearly a blank. In 1906, when Handlirsch published his revision of the fossil insects of the world, only 14 specimens, aside from cockroaches, had been described from the strata of this period. But in recent years the discovery of new and highly productive Permian beds has added so many well preserved fossils to this record that our knowledge of the Permian fauna is rapidly surpassing that of the other Pre-tertiary horizons.

Most of these new fossils have been secured in the Lower Permian beds of Kansas, which have already yielded upwards of 6000 specimens. The first insects were found in this deposit in 1899. During the winter of that year Dr. E. H. Sellards found two fossil wings in a collection of plants which he had obtained in the Wellington shales, just south of the town of Elmo, Kansas. Realizing the significance of his discovery he returned to the locality during the summers of 1902 and 1903, and after some difficulty in locating the proper layer, secured about 2000 specimens. At that time the taxonomy of fossil insects was in a deplorable condition. Handlirsch's work, which for the first time placed the classification of the extinct forms on a solid foundation, had not yet appeared, and the literature on the subject was extremely fragmentary and scattered. But between 1906 and 1909 Dr. Sellards published three papers on his collection, describing a few of the forms which seemed to be typical of the fauna. It was his intention at that time to publish a revision of the fossils, but other matters intervened and for many years this huge collection was stored in his home at Austin, Texas. In the spring of 1927 when I was enabled by a grant

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from the National Academy of Sciences to make an extended visit at Austin, Dr. Sellards kindly placed his types at my disposal for examination, and the following year he sent me his entire unworked collection for study at the Bussey Institution.

Meanwhile, a second collection of insects had been obtained at the Elmo deposit. Dr. R. J. Tillyard, the eminent entomologist of the Cawthron Institute, New Zealand, had passed through this country in 1920, and while visiting Yale University had seen a small series of the Kansan specimens which Dr. Sellards had donated to the Peabody Museum many years ago. Tillyard aroused Professor Schuchert's interest in these insects, and the following summer Professor C. O. Dunbar undertook an expedition to the locality. He returned with a collection of about 2000 specimens, which were immediately sent to Dr. Tillyard for study. During the past four years Tillyard has published eleven papers on this fauna, covering the Palaeodictoptera, Mecoptera, Protohymenoptera, Homoptera, Psocoptera, Protodonata, Odonata, and Protoperlaria. All the Yale specimens have remained the property of the Peabody Museum, with the exception of the counterparts of some of the types, which have been given to the Cawthron Institute.

In the fall of 1925 I accompanied Professor P. E. Raymond to the Kansan locality to determine whether or not another large collection of insects could be obtained at these beds. Our short stop at the deposit was sufficient to obtain an affirmative answer to this question (Carpenter, 1926), and two years later, with the financial aid of a Sheldon Traveling Fellowship and the assistance of two graduate students in entomology, I secured some 2400 specimens, comprising the third and largest collection from this formation. All these fossils are now at the Bussey Institution, but they will be turned over to the Museum of Comparative Zoölogy when my description of them has been completed.

The deposit which has yielded these splendid collections is situated in Dickerson County, Kansas, within the township of Elmo, and about three and one-half miles southwest of the town itself. The rock containing the insects, termed the "Elmo limestone" by Dunbar, has been found only in a pasture covering about thirty acres (Plate 1, fig. 1). This pasture has the typical rolling topography of central Kansas, so that there are very few natural exposures of the limestone, or in fact of any part of the Wellington series. A few meandering brooks have cut occasional gullies, but these are rarely over a few feet deep. All the Harvard and Yale specimens were obtained near the center

of the pasture, but Sellards' collection was taken about a quarter of a mile farther south. Fully half of the Harvard fossils came from the north side of a small ravine about twenty feet southwest of the gully which produced the Yale specimens; the remainder were taken in the west bank of Dunbar's quarry of 1921.

The stratigraphy of the Wellington shale in this region has been carefully worked out by Dr. Dunbar, and I can add nothing new to his excellent account (Dunbar and Tillyard, 1925). At both of the exposures where we collected in 1927, the Elmo limestone was capped by a few feet of a limy shale, unfossiliferous except for a few phylopod crustaceans. The Elmo limestone itself is a chalky, soft, almost white deposit, about five feet thick; only the very bottom, more massive layer of this stratum contains insects (Plate 1, figs. 2, 3). Just below the insect layer, extending down for a depth of about three feet, is a very soft, carbonaceous clay, containing many matted fronds and stems of land plants, and occasional large stumps of *Psaronius*<sup>1</sup> (Plate 1, fig. 4). Throughout the insect layer of the Elmo limestone there are a number of fragments of plants, a few arachnids, and one species of clam, *Myalina meeki* Dunbar. The latter is the commonest fossil, especially in the very basal part of the limestone, where the shells are crowded together in huge masses. Dunbar observed in his description of the beds that the insects and *Myalina* were mutually exclusive on any one layer of the rock, but this is certainly not true at all exposures. Another common fossil in the insect layer has the appearance of a pink alga, which seems to occur almost uniformly at about the same level. For some curious reason the insects are very closely associated with this fossil, or at least with the layer of rock on which it occurs; sometimes as many as twelve insects have been found on a square foot of this surface. The arachnids, *Eurypterus* and *Paleolimulus*, are quite rare, but are also associated with the insects. About fifty specimens of these two genera were taken in 1927, and have been turned over to Professor P. E. Raymond, of the Museum of Comparative Zoölogy. The plants of the insect layer are too fragmentary for accurate determination. Sellards described the flora of the Wellington shale in this region many years ago (1908), but a more complete account is contained in a monograph by David White, now in press.

The insects have a very sporadic horizontal distribution in the limestone. Some portions of the insect layer, only a few feet away from a rich pocket, seem to be almost devoid of specimens; or if the insects are present, they are badly macerated and poorly preserved. Our ex-

<sup>1</sup> Determined by Dr. David White.

perience in collecting leads us to the conclusion that these fossils can be obtained more easily if the rock is dry. When the limestone is damp, as it ordinarily is directly after its removal from the ground, its color is dark gray, and the minute insects, such as the Psocids, can be seen only with difficulty. The dry rock, however, is almost a chalky white, so that the insects can be seen much more readily. The dry limestone also has the advantage of splitting more evenly.

The climatic conditions which prevailed at the time of the existence of an extinct biota are always of interest and sometimes of great significance to the biologist. Dr. Dunbar's study on the geology of the formation leads him to conclude that the environment of the insects was a "swampy, forested lowland. This local moist habitat appears, however, to have been a humid spot in a regional environment of more or less pronounced and long-continued aridity, for the preceding strata of the entire province are marked by extensive saline deposits. The earlier stages of the Permian were characterized, over the Great Plains Province, by the alternating seasonal rainfall and droughts of a semiarid climate, and from this mild beginning the aridity gradually became more severe until it reached a climax in Wellington time, when the excessive evaporation of the inland sea resulted in the precipitation of thick salt beds over central and southern Kansas. Our insects lived shortly thereafter, at a time when the climate had again become somewhat ameliorated. The cold climate of the later part of the Lower Permian had not yet affected the region of Kansas, where decidedly warm temperatures still prevailed, and it is improbable that the insects of this portion of the United States had ever endured cold winters."

Since the Wellington shale has been definitely referred to the Lower Permian (Middle Artinskian), the insects of the Elmo limestone are the oldest of any of the Permian forms which have been found.<sup>1</sup> Only two other Permian formations have produced notable collections of insects. The Belmont cherts of New South Wales, which belong to the highest part of the Permian, have yielded a small but interesting series of Mecoptera, Neuroptera, Coleoptera, Homoptera, and Protocoleoptera (Tillyard, 1917, 1919, 1922, 1926); and the Upper Permian (Kazan) of North Russia has produced a varied fauna of Homoptera, Mecoptera, Neuroptera, Psocoptera, Protorthoptera, and a few extinct groups allied to the Perlaria (Martynov, 1928). The researches which have been conducted on these Permian insects, especially those of Till-

<sup>1</sup> Except, perhaps, the Hermit shale of the Grand Canyon, which has yielded two species of Protodonata (see White's note on the flora of the Hermit shale, Proc. Nat. Acad. Sc., 13 (8), p. 574-575, 1927).

yard's on the Kansan forms, have filled in many gaps in the phylogenetic tree of the insects. Yet our knowledge of these ancient types is still very meagre. Practically nothing is known of their body structure, and in many cases only portions of the wings have been found. Under such conditions it is only natural that some erroneous conclusions have been reached, but by the study of additional material most of these will be eliminated, and our conception of the geological history of the insects will become more exact. Consequently, although among the 4400 unstudied fossils now at my disposal, there are only a few new species, the addition of many details to those already known in the described forms, will, I hope, clear up some of the uncertainties and remove some of the inaccuracies which now exist. Since Tillyard has treated the Yale insects by orders, completing one group before starting on another, I propose to adopt the same method. This procedure was suggested to me by Dr. Tillyard in order that I might publish on the Palaeodictyoptera, Protohymenoptera, Psocoptera, Odonata, Protodonata, Mecoptera, Homoptera, and Protoperlaria, without in any way interfering with the investigations which he is now carrying out on the other orders. His earlier start on the Kansan insects should give him that priority.

It is a pleasure to acknowledge my gratitude to those who have aided me in this undertaking. To Professor W. M. Wheeler I am deeply indebted for the interest which he has taken in the progress of the investigation, and especially for the encouragement which he has always been ready to offer. To Professor E. H. Sellards, of the University of Texas, I am under lasting obligation for his courtesy in allowing me to study the types in his collection, and for the loan of the rest of this valuable assemblage of fossils. Sincerest thanks are also due to Mr. and Mrs. E. E. Bert and their family, of Abilene, Kansas, for many kindnesses extended while I was collecting at the Elmo deposit. To Messrs. J. W. Wilson and W. S. Creighton, of the Bussey Institution, I am more than grateful for their assistance in the field, as well as for the care which they employed in collecting the fossils with me in 1927.

#### THE ORDER MECOPTERA

The existing Mecoptera are but a remnant of the large series of forms which existed during the early Mesozoic and the Permian. Less than two hundred living species have been found over the world, and some monospecific genera, as *Merope* and *Notiothauma*, seem to be on the verge of extinction. The recent representatives of the order are

widely distributed, as one would expect, although the primitive groups are restricted to small areas. The family *Panorpidae* occurs throughout the North Temperate regions, the *Bittacidae* have been taken in all parts of the world, and the *Boreidae* range over Europe and North America. The *Nannochoristidae*, which possess a peculiar combination of specialized and primitive characteristics, are limited<sup>1</sup> to Australia, Tasmania, and New Zealand; the *Choristidae* are restricted to Australia; the monospecific family *Meropidae* is found only in eastern United States; and the *Notiothaumidae*, an obscure family known only from three individuals, is confined to parts of Chile.

Although the geological history of the order was very obscure less than a decade ago, it is now better known than that of any other group of holometabolous insects. Both the *Panorpidae* and *Bittacidae* are represented in the Tertiary of Europe and North America, and the latter family is also present in the Jurassic of Turkestan (Martynov, 1928; Carpenter, 1928). No other living families have been recognized in the Mesozoic rocks, but the extinct family *Orthophlebiidae* and its allies, which are closely related to the *Panorpidae*, have been found in the Jurassic of England, Germany, and Turkestan. The best specimens of these orthophlebiids have been taken in the Turkestan beds, and are especially interesting because they possess the long beaks characteristic of the more highly specialized modern Mecoptera. The next oldest record in the history of the order is that of the Triassic of Queensland, which contains three families, *Stercochoristidae*, *Mesochoristidae*, and *Archipanorpidae*. The two former families are related to the recent choristids, but the affinities of the *Archipanorpidae* are not clear. In the Upper Permian beds of New South Wales the family *Mesochoristidae* is still present, together with the *Belmontidae*, which are considered by Tillyard to belong to a distinct but related order, the *Paramecoptera*. The Upper Permian of Russia (Kazan), the fauna of which has recently been monographed by Martynov (1928), contains two genera strikingly similar to *Agetopanorpa*, new genus, from the Lower Permian of Kansas. Since I do not agree with Martynov on the affinities of the Russian Permian Mecoptera, I shall discuss these fossils more thoroughly after the description of the Kansan forms.

The Lower Permian of Kansas has yielded the earliest unquestionable records of true Mecoptera.<sup>2</sup> The Yale collection from this forma-

<sup>1</sup> Since this was written, the family has been found in South America.

<sup>2</sup> Tillyard regards the Carboniferous *Metropator pusillus* Handl. as a true Mecopteran, but this classification is open to question. See Crampton (C.G.), Bull. Brooklyn Ent. Soc., **22**, p. 12-13, 1927.

tion includes sixteen specimens, placed by Tillyard (1926) in fourteen species, and the small collection which the Museum of Comparative Zoölogy obtained in 1925 contained a single individual. The unstudied material now at my disposal includes thirty-eight specimens of this order, one of which is in Dr. Sellards' collection, and thirty-seven in the Harvard collection. As one would naturally suppose, these new fossils add much to our knowledge of the Permian Mecoptera, especially since many of them are extraordinarily well preserved. All the specimens which have previously been known from the Kansan beds consist of isolated wings, but fully half of the Harvard fossils possess fore and hind wings and portions of the bodies.

In addition to the Mecoptera in the Harvard and Sellards' collection, I have been able, through the kindness of Professor C. O. Dunbar, to study Tillyard's types at the Peabody Museum. To Dr. Dunbar I am also grateful for the use of apparatus which enabled me to examine these fossils under the best of conditions, and especially for the use of photographic equipment. Professor Dunbar also gave me permission to remove several bits of rock matrix which obscured portions of some of the types. The exposing of the hidden parts has added many important points to our knowledge of the species, and in the case of one fossil, *Protopanorpa pusilla* Till., has shown so many unexpected characteristics that a distinct family must be established for it.

Tillyard has already discussed the wing venation of the Mecoptera and its evolution in the *Panorpid Complex* (1919), but since much additional material, both fossil and recent, has been accumulated in late years, it seems advisable to review the subject at this time. In the fore wing of all recent Mecoptera, the subcosta is apparently unbranched, although in *Chorista* it is connected distally to the costal margin by an oblique veinlet. This veinlet, in my opinion, is the vestige of an anterior branch of the forked subcosta which is present in the *Permopanorpidae*, *Permochoristidae*, etc. R1 usually possesses one or more distal veinlets which run through the pterostigmatic area, and in the older fossil Mecoptera these veinlets are distinctly dichotomous in their origin. A number of genera, however, even the Permian *Petromantis* and *Agetopanorpa*, new genus, have R1 unbranched. The radial sector is a well developed system, originally possessing four main branches, each of which, in the more primitive groups, is forked at least once, so that as many as ten terminal branches may result. In the highly specialized forms, as *Nannochorista*, the number of terminal branches is only three. The media divides basally into M1-4 and M5, the latter being partly present as a free vein in only the

primitive genera, where it forms the upper arm of the Cu-M Y-vein. In *Platychorista* there may be as many as nine terminal branches to M1-4, but in all recent Mecoptera there are not more than four terminal branches (normally). The cubitus divides basally into Cu1 and Cu2, the former diverging upwards to fuse with M5, forming a composite vein, M5+Cu1, which leads directly to the posterior margin of the wing. Tillyard has always regarded this vein as being unbranched in all Mecoptera, but as a matter of fact it is distinctly forked in *Platychorista venosa* Till., as will be shown later. Cu2 is a simple vein in all known forms. The three anal veins are free, and either forked or simple. The Cu-M Y-vein is the most important phylogenetic structure in the wing. The basal stem of the "Y" is formed by the composite vein, M5+Cu1, the right arm by the free part of M5, and the left arm by the free piece of Cu1. The primitive condition of this structure is best seen in the *Permopanorpidae*, *Platychoristidae*, and *Meropidae*, both M5 and Cu1 being equally well developed. A somewhat higher stage is represented by *Permochorista*, *Panorpodes*, and *Panorpa*, in which M5 is shortened and has assumed the position of a cross-vein. The next step is present in *Chorista*, M5 having almost disappeared, and the most highly specialized condition is found in *Bittacus*, in which Cu1 has fused for a short distance with M1-4, and M5 has completely vanished.

The hind wing is similar to the fore, but is by no means identical. It is always shorter and more narrowed basally; the subcosta is shorter than that of the fore wing; and in all recent forms 1A and Cu2 are fused for a short distance. M5 is not present as a free vein in the hind wing of any known Mecopteran; even when this structure is well developed in the fore wing, it is entirely missing in the hind pair. Since none of the specimens of Mecoptera in the Yale collection had both pairs of wings preserved, Tillyard was not able to determine just how much the venation of the hind wing had been modified by the time of the Lower Permian. He considered it probable that the fusion of 1A with Cu2 had not then been reached, and he also assumed that M5 was a free vein, the Cu-M Y-vein being completely formed as in the fore. The fossils in the Harvard collection show that the fusion of 1A with Cu2 had not been attained in the Permian forms, but that M5 was entirely absent, Cu1 joining the stem as in recent Mecoptera. Tillyard has already observed (1919) that the "main line of evolution within the Mecoptera has been by narrowing of the wings, with suppression of the original archaic branches of Rs and M1-4. With the narrowing there has proceeded also a lengthening process, which culminates in such forms as the *Bittacidae*." If we bear in mind that the



hind wing in all known forms is somewhat ahead of the fore wing in the narrowing process, it is not surprising to find M5 absent in the Permian Mecoptera, even though it has disappeared in the fore wing of only the highly specialized recent groups.

The Mecoptera in the Yale collection were separated by Tillyard into three families: *Protomeropidae*, *Permopanorpidae*, and *Anormochoristidae*. Unfortunately, one change must be made in this arrangement. The genus *Protomerope* Till. is synonymous with *Platychorista* Tillyard (placed by him in the *Permopanorpidae*), so that because of page precedence the family name of this Merope-like insect must become *Platychoristidae*. Two additional families, *Agtopanorpidae* and *Lithopanorpidae*, are established in this paper, the former for a new species in the Harvard collection, and the latter for Tillyard's *Protopanorpa pusilla*.

### PLATYCHORISTIDAE

Small insects, allied to the recent *Meropidae*.

*Fore wing*.—Costal space broad, traversed by a number of oblique veinlets leading to the costal margin from Sc, and also from the part of R1 in the pterostigmatic area; pterostigma weakly developed; Rs and M with numerous dichotomous branches; Cu-M Y-vein strongly formed; Cu1+M5 forked distally; Cu2 unbranched, terminating on the posterior margin of the wing; 1A looped to Cu2 and 2A looped to 1A, distally.

*Hind wing*.—Shorter than the fore wing, and more narrowed basally; costal space much narrower than that of the fore wing, traversed by a small number of veinlets; Sc shorter than in the fore wing; branching of Rs and M similar to that of the fore wing; Cu-M Y-vein absent; Cu1+M5 simple, joined directly to the stem of the media; Cu2 forked; 1A unbranched, 2A forked.

Macrotrichia are well developed on the main veins of both wings.

Prothorax small, apparently not prolonged over the head as in *Merope*. Female with a rather robust, tapering abdomen, terminating in a pair of short cerci; male with a much shorter abdomen, apparently terminating in a pair of small claspers.

### PLATYCHORISTA Tillyard

*Platychorista* Tillyard, Amer. Journ. Sci., **11** (62), p. 154, 1926.

*Protomerope* Tillyard, Amer. Journ. Sci., **11** (62), p. 157, 1926.

*Fore wing*.—Costal space narrowed basally; hm present; Sc reaching to the pterostigma and terminating in a short fork, one branch of which

leads to the apical margin, the other to R1; Rs with ten or twelve branches, variable in their arrangement; R straight basally, but with a distinct downward bend before the origin of Rs; M with nine to eleven branches, variably arranged; Cu-M Y-vein with a straight upper arm (M5) and a sigmoidal lower arm (Cu1), which is more than twice as long as the upper. Cross-veins few and weakly developed.

*Hind wing*.—Costal space only slightly narrowed basally; hm present; Rs and M branched essentially as in the fore wing; Rs straight basally, but with the bend much nearer the base and more abrupt than in the fore wing; Rs originating at the apex of this bend; Cu1+M5 and Cu2 very close together, almost fused; both Cu1+M5 and Cu2 fused with M basally; cross-veins apparently more weakly formed than in the fore wing.

*Genotype*.—*Platychorista venosa* Till.

#### PLATYCHORISTA VENOSA Till.

Plate 3, fig. 1; Plate 4, fig. 2

*Platychorista venosa* Tillyard, Amer. Journ. Sci., 11 (62), p. 154, 1926.

*Protomeroper permiana* Tillyard, Amer. Journ. Sci., 11 (62), p. 159, 1926.

Length of female (excluding head), 3.6 mm.; length of male (excluding head), 2.5 mm.

*Fore wing*.—Length, 5.6 mm.; greatest width, 1.7 mm.; elongate oval, the apex well rounded, the center of the apex falling on the longitudinal axis of the wing; subcostal veinlets, 10-12, usually more oblique apically than basally; R at base variable with respect to the amount of bend before the origin of Rs; pterostigma rather short, unpigmented, with 4 or 5 veinlets; R very straight after the origin of Rs until it reaches the pterostigma, where it makes a second bend; R2 with 2-4 branches; R3 and R4 with 2 branches; R5 with 2-4 branches; M close to R at base, M5 separating off just before the origin of Rs; M1+2 diverges from M3+4 just a little basal of the first division of Rs; M1, M2, and M3 with 2 branches; M4 with 3-4 branches; the free basal part of Cu1 is nearly parallel with the longitudinal axis of the wing; the fork of Cu1+M5 is rather deep, going back nearly as far as the first branch of M4; Cu2 and 1A almost parallel and rather close together for their entire lengths; 1A unbranched; 2A and 3A apparently widely forked distally; a very strong, sigmoidal cross-vein is present between R1 and Sc, just apically of the origin of Rs; the other cross-veins seem to be quite variable in position.

*Hind wing.*—Length, 5.0 mm.; greatest width, 1.3 mm.; well rounded apically, the center of the apex a little anterior of the longitudinal axis of the wing; only 3 or 4 subcostal veinlets; Sc terminating in front of the pterostigmata; R1 gently curved sigmoidally after the origin of Rs, so that it very nearly touches Sc just above the first division of Rs; pterostigma a little longer than in the fore wing, with 2 or 3 veinlets, but no pigmentation; Rs originating very close to the base of the wing, dividing soon after into its main branches; R2 and R3 usually divide directly above the separation of R4 and R5; M separates into M1-4 and M5 apically of the first division of Rs; the branches of M1-4 usually resemble those of the fore wing; Cu1+M5 is much crowded distally between Cu2 and the posterior branch of M4, but it disappears into the wing membrane before reaching the wing margin; 2A forks at about half its length; 3A unbranched. The costal space, including the pterostigmatic area, bears 4 small circular eye-spots, the first and smallest at the first veinlet, the second on the next veinlet, the third on the following veinlet, and the fourth in the middle of the pterostigma.

The thorax is quite broad, with a small prothorax. The first four abdominal segments of the female are about as broad as long, the others much longer than broad, although the length of these segments is undoubtedly dependent upon the degree of contraction of the abdomen. The cerci on the 10th segment are well developed, but the exact number of segments is not definitely known. The external genitalia of the male of this species are preserved in one specimen in the Harvard collection (3007ab). They are in the form of short claspers, somewhat similar to those of *Merope*, but much smaller.

*Holotype.*—No. 5067 (hind wing), Peabody Museum. Specimens Nos. 5069a and 5070b in the Yale collection, described by Tillyard as the holotype and paratype (respectively) of *Protomerope permiana*, are fore wings of this species.

The Harvard collection contains eight specimens, as follows: no. 3001ab,<sup>1</sup> a complete fore wing, very well preserved, collector, F. M. Carpenter. No. 3002ab, complete fore wing, splendid preservation; collector, F. M. Carpenter. No. 3003ab, apical two-thirds of fore wing; collector, F. M. Carpenter. No. 3004ab, complete fore wing, fairly well preserved. No. 3005ab, complete fore wing; collector, J. W. Wilson. No. 3006ab, a female, consisting of the basal portions of the fore wings, and the body complete except for front of head; collector, F. M. Carpenter. No. 3007ab, a male, consisting of all four wings and body, except head; collector, F. M. Carpenter. No. 3008ab, probably female,

<sup>1</sup> The letters "ab" indicate the presence of both obverse and reverse.

fore wing complete, most of hind wings, and portions of body; collector, W. S. Creighton.

As I have indicated above, Tillyard described the hind wing of this insect as *Platychorista venosa*, which he considered to be the "highest evolutionary type" within the family *Permopanorpidae*. The fore wing he described as *Protomerope permiana*, placing it in a separate family, *Protomeropidae*, which he regarded as directly ancestral to the recent *Merope*. Fortunately, the complete specimens in the Harvard collection enable us to correlate these two wings. It will be observed, however, that my description of the fore and hind wings differs in many respects from Tillyard's. In the fore wing Tillyard described an unbranched Cu1, whereas I have figured it as being forked. Every one of the eight specimens in the Harvard collection has this vein forked, to the same degree and with the same distinctness. Specimen no. 5069a in the Peabody Museum (the holotype of *Protomerope permiana*) is lacking a bit of the wing near the termination of Cu1, including the area occupied by the anterior fork, so that Tillyard could not know from this fossil whether the vein was branched or not. The other specimen of the fore wing in the Yale collection (No. 5070a, the paratype of *Protomerope permiana*) is much better preserved and shows the distal fork of Cu1+M5 so clearly that I do not understand how Tillyard could have overlooked it. Tillyard also stated that in the fore wing 1A terminates on Cu2, as shown in his figure. But as a matter of fact, his 1A is really 2A, and his 2A is 3A, for there is another vein, the true 1A, situated between Cu2 and his so-called 1A. This true 1A is very faintly preserved in the Yale specimen numbered 5069a, but is quite distinct in the other fossil. In the hind wing, the free piece of Cu1 is not present, although Tillyard has indicated it in his figure; instead, Cu1+M5 joins M at the very base of the wing, as in all other known Mecoptera. I examined his holotype of *Platychorista venosa* with the greatest care, but could not find the slightest trace of a free basal piece of Cu1, and could not find it in any of the Harvard specimens. Cu1+M5 is a weakly developed vein, parallel and very close to Cu2; this peculiar condition is not due to distorted preservation, for it is found in all the hind wings in the Harvard collection, and in the Yale holotype as well, although it was overlooked there by Tillyard. Cu2 is really forked, not unbranched as described by him. The peculiar concavity of the anterior margin of the wing as drawn by Tillyard is merely the result of the distorted position in which the insect lies on the rough rock. The holotype specimen at Yale shows distinctly the four small eye-spots on the costal space, although these are not mentioned in Tillyard's description.

In working out the venation of this insect I was somewhat disconcerted by the variability of the structure of the radial sector. Some of the different types of branching which occur are shown in text figure 1. It will be observed that the position of the origin of Rs, as well as

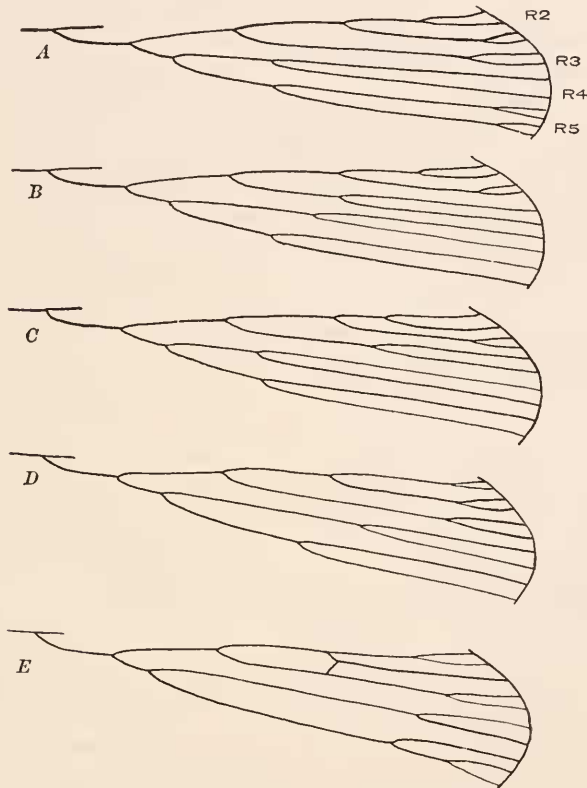


FIG. 1.—Variations in the radial sector of *Platychorista venosa*: A, No. 3003; B, No. 3004; C, No. 3005; D, No. 3007; E, No. 5669 (Yale).

the point of origin of each of the four main branches of this vein are constant; the variation takes place in the number and position of the additional forkings. A similar but less marked variation takes place in the radial sector and media of the recent *Merope tuber*.

The new specimens of *Platychorista venosa* contained in the Harvard collection have added so many details to our knowledge that we are

now in a position to consider fairly accurately its affinities. Tillyard regarded *Protomerope*, which he based upon the fore wing of this species, as "undoubtedly the direct ancestor of the recent North American genus *Merope*, and probably also of the South American genus *Notiothauma*." As far as the fore wing of *Platychorista* is concerned this might be true, for even the fork on Cu1+M5 only means that the genus is a little farther down the phylogenetic tree of the Panorpid orders than Tillyard supposed, and much closer to the archetype of the complex. But from the evidence afforded by the hind wing I cannot agree that this genus is in the line of direct ancestry of *Merope* or *Notiothauma*. In the hind wing of *Merope* the cubitus originates and divides in a manner not very unlike that of *Panorpa* and the other recent Mecoptera, the basal part of Cu1 being fused to the media, and the corresponding part of Cu2 being fused to 1A. The very close association of Cu2 with Cu1+M5 in *Platychorista* is a specialization which certainly could not have given rise to the perfectly normal structure in *Merope*. The crowded condition of Cu1+M5 distally is a high specialization found in no other Mecopterous forms, although it does recall the more advanced state in *Stereochorista frustrata* Till., from the Upper Triassic of Ipswich, Queensland. The obvious conclusion is that although *Platychorista* is certainly the closest relative of *Merope* that has thus far been found as a fossil, it is too highly specialized along other lines to enable us to place it as the ancestor of *Merope*. It is more probable that the family *Platychoristidae* is an end branch which diverged from the true ancestors of the *Meropidae* during the earlier Permian or perhaps the Upper Carboniferous.

Tillyard also pointed out that there are many resemblances between *Platychorista* and the primitive Neuroptera, and concluded that the Lower Permian ancestor of the Neuroptera must have been closely allied to *Platychorista*. The additional characteristics of the fore wing which have been presented here serve to substantiate this conclusion. The distal forking of Cu1+M5 and the termination of 1A on the wing margin are features of the archaic Neuroptera. At the time when Tillyard's suggestion was made, the oldest known Neuroptera were the *Permithonidae*, from the Upper Permian of Australia, but recently several other Neuroptera have been described from the Russian Permian by Martynov (1928) and Zalessky (1926). The venation of one of these species, *Palacomerobius proavitus* Mart., is strikingly similar to that of *Platychorista*, being more specialized only in the twigging of the main branches, and the loss of M5. It is obvious, however, from the absence of the Cu-M Y-vein in the hind wing of *Platychorista*, and its normal development in the hind wing of the

primitive recent Neuroptera, that this Lower Permian genus cannot have been directly ancestral to the order Neuroptera.

### PERMOPANORPIDAE

Minute insects related to the recent *Panorpidae* and *Choristidae*.

*Fore wing* (known in *Permopanorpa* and *Protopanorpa*).—Shape much as in *Panorpa*; costal space narrow or fairly broad, traversed by a small number of veinlets; humeral cross-vein always present; pterostigma well developed; Sc forked distally; R1 strongly formed, usually with one or more pterostigmatic veinlets; Rs with from 4-9 terminal branches, also dichotomous; Cu-M Y-vein well developed; Cu1+M5 strongly formed, unbranched, straight or nearly so; Cu2 weakly formed, unbranched, usually gently curved; 3 anal veins present, somewhat variable in position and termination.

*Hind wing* (known in *Protochorista* and *Permopanorpa*).—Shorter than the fore wing, and more narrowed basally; costal space as in the fore wing, but Sc much shorter; branches of Rs and M as in fore wing; Cu1+M5 leading directly to the base of M, the Cu-M Y-vein being entirely absent.

The main veins of both wings are pitted with the large bases of macrotrichia, which are themselves very well preserved in many of the Harvard specimens. Tarsi 5-segmented, the basal segments being markedly longer than the others, as in all recent Mecoptera; legs with two tibial spurs, and coated with hairs as in recent Mecoptera, but without the numerous spines on the tibiae present in the *Panorpidae*. Female with a pair of short cerci protruding from the end of the abdomen, and possessing at least 3 segments; male with short, protuberant genitalia, closely resembling those of the recent *Bittacidae*.

This family was established by Tillyard to include four genera from the Kansan Permian, *Permopanorpa*, *Protopanorpa*, *Protochorista*, and *Platychorista*. The latter genus belongs to a separate family, corresponding to Tillyard's *Protomeropidae*, as I have shown above. Martynov also placed in the *Permopanorpidae* the genera *Petromantis* and *Kamopanorpa* from the Russian Permian, but these, together with a new Kansan genus, belong to a distinct family, described below.

### PERMOPANORPA Tillyard

*Permopanorpa* Tillyard, Amer. Journ. Sci., **11** (62), p. 143, 1926.

*Fore wing*.—Elongate, well rounded apically; costal space narrow, very slightly concaved, nearly straight; Sc terminating on the costal

margin before the pterostigma, its anterior distal branch much reduced; R1 straight, with 1-4 pterostigmatic veinlets; pterostigma elongate, but somewhat variable in size; Rs with from 5-9 terminal branches; M with 6 terminal branches, constant in their arrangement; M1 and M2 forked distally, M3 and M4 unbranched; Cu-M Y-vein with the free part of Cu1 about twice as long as M5; number and arrangement of cross-veins variable.

*Hind wing*.— Sc terminating on the costal margin before the middle of the wing; pterostigma shorter than in the fore wing; Rs originating nearer to the base than in the fore wing; branching of Rs and M as in the fore wing; Cu1 diverging from Cu2 close to the base of the wing, the free part of Cu1 being oblique and weakly developed; 3 anal veins, 1A fused with 2A for a short distance. Head with a small beak, about as long as that in *Chorista*; eyes large, rounded, not protuberant; antennae with 16 segments; body with about the same habitus as that of *Panorpa*; legs about as slender as those of *Panorpa*, the prothoracic pair being somewhat shorter than the others.

*Genotype*.— *Permopanorpa formosa* Till.

This genus, as observed by Tillyard, is closely related to the recent *Panorpidac*, *Choristidac*, and the extinct *Orthophlebiidac*. It cannot, however, be in the line of direct ancestry of any of these families, since the media is developed in quite another direction. In the hind wing, also, the fusion of 1A with 2A is a specialization which could hardly have produced the type found in the three families mentioned.

In the Yale collection Tillyard found seven specimens belonging to this genus, each of which he assigned to a distinct species. These species were separated on such characters as the relative lengths of the arms of the Cu-M Y-veins; the presence or absence of pterostigmatic veinlets and the anterior branch of the subcosta; and the number of terminal branches to Rs. Shortly after the description of the Yale species, I described the one which the Museum of Comparative Zoölogy obtained in 1925 as *P. raymondi*, using the same distinguishing characteristics as Tillyard had employed. Of this series of eight species, *P. formosa*, as described by Tillyard, differs markedly from the rest by its relatively large size, and *P. schucherti* is made distinctive by its peculiar system of cross-veins. When I began to study the 24 specimens in the Harvard collection which belong to this genus, I observed that in every one the arms of the Cu-M Y-vein were unequal, Cu1 always being about twice as long as the free part of M5. It seemed advisable, therefore, to examine Tillyard's types in the Peabody Museum, and this I was able to do through the kindness of Dr. Dunbar. This



study of the types showed conclusively that the Cu-M Y-vein in *P. tenuis*, *dunbari*, and *sellardsi* was formed exactly as in *gracilis* and *inaequalis*, with the arms unequal, not equal, as stated by Tillyard. A photograph of the type of *P. tenuis*, which shows clearly the structure of the Y-vein, is reproduced here for reference. This constant form of the Y-vein aroused my suspicions as to the validity of *P. gracilis*, *P. inaequalis*, *P. tenuis*, *P. dunbari*, and *P. sellardsi*, and induced me to examine the types with particular attention to the other characteristics which Tillyard selected as specific. My notes on these specimens follow:

1. The type of *P. inaequalis* is not quite as Tillyard figured it.<sup>1</sup> Rs joins the stem of R at the lowest point in the bend of R, just as it does in *gracilis*, *sellardsi*, and the others. The vein which Tillyard calls R4b actually diverges from R5, and is only joined to R4 by a cross-vein. In my opinion the peculiar shape of the wing of *inaequalis* is merely due to distortion, the specimen being on a rough rock surface and poorly preserved, as mentioned by Tillyard.

2. In addition to the form of the Cu-M Y-vein as already mentioned, the type of *P. tenuis* deserves some comment. The pterostigma is faintly preserved, and, since the greater part of it is missing, there may very possibly be veinlets present. The small piece of rock which originally covered a portion of the hind margin of the wing was removed with a fine needle, exposing a simple M4, as in *inaequalis*.

3. The type of *P. gracilis* is exactly as Tillyard described it, but I believe that the small indentation of the hind margin, which he figures at the termination of 3A, is merely due to a slight wrinkle in the wing membrane.

4. In the type of *P. dunbari*, the pterostigma is so darkly pigmented that even if veinlets were present they could not be discerned. Tillyard stated in his description that the basal portion of the wing was obliterated, but as a matter of fact it was only covered up by a small chip of the limestone, which was easily removed by a fine needle. This part of the venation turned out to be the same as that of *P. inaequalis*.

5. In the type of *P. sellardsi* the subcosta is forked distally. The Cu-M Y-vein is exceedingly faint, but a careful scrutiny of this structure brought me to the conclusion that the arms of the "Y" are unequal, as mentioned above.

It is clear from these observations on the types that the Yale speci-

<sup>1</sup> The figures of *P. tenuis* and *inaequalis* are incorrectly labeled in Tillyard's paper (Amer. Journ. Sci., 11 (62), p. 146-147). Fig. 8 is *P. tenuis* and Fig. 9 is *inaequalis*, and the descriptive titles under these illustrations should be interchanged.

mens are much more alike than Tillyard supposed. The subcosta is forked in all; the pterostigmatic veinlets are present except when the wing is poorly preserved or the pterostigma so heavily pigmented that

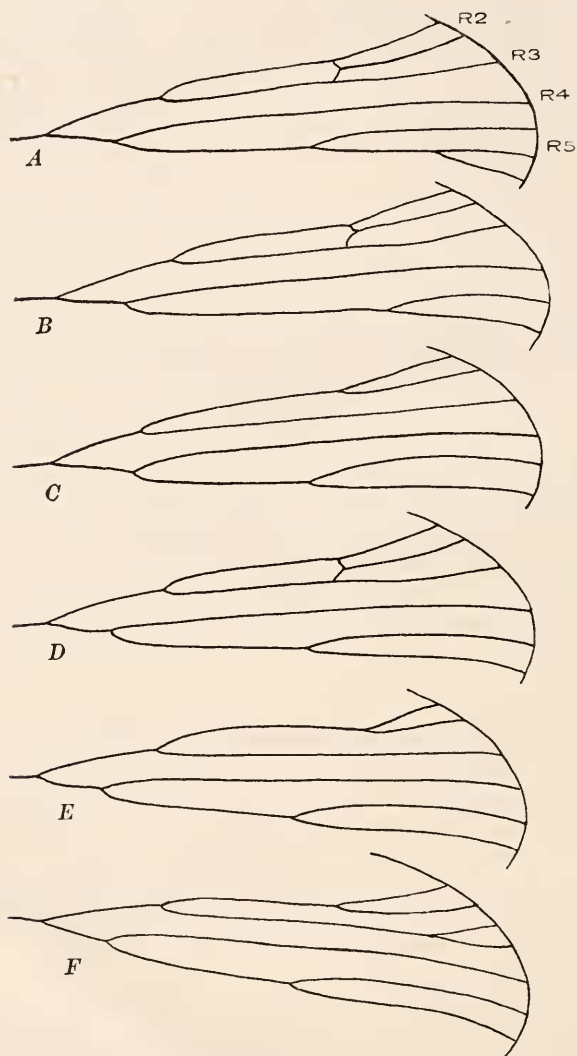


FIG. 2.—Variations in the radial sector of *Permopanorpa inaequalis*:  
A, No. 3021; B, No. 3016; C, No. 3010; D, No. 3019; E, No. 3018;  
F, No. 3013.

they cannot be seen; and the arms of the Cu-M Y-vein are identical in size and shape. When I continued my examination of the Harvard fossils, I was surprised to find slight and inconsistent differences in the branching of the radial sector, in the number of cross-veins between Sc and the costal margin, and in the degree of development of the anterior branch of Sc. A few variations of the media possessed by the Harvard specimens are shown in text figure 2, and others can be seen in Tillyard's illustrations. No two wings in the Harvard or Yale collections are alike in venation, and no two variations can be correlated or coupled. There is also some diversity in the shape of the wings, but allowing for distortion during preservation this is no greater than in many of our existing species of *Panorpa*. The only actual difference between all these specimens is in the number of terminal branches on the radial sector. If we recognize each of these types of branching as of specific rank, we must place every specimen in the Harvard and Yale collections into a distinct species. This procedure would be as absurd as assigning all the specimens of *Lemmatophora typa* Sell., of the Kansan beds, to separate species (Tillyard, 1928). The only alternative is to consider all these fossils as representing a single species with a variation more marked than in recent Mecoptera, yet quite consistent with that which we find in most ancient insects. This evidence places *P. inaequalis*, *tenuis*, *gracilis*, *dunbari*, *sellardsi*, all described by Tillyard, as well as *P. raymondi* Carp., into a single species, which must be named *inaequalis*, by page precedence.

#### PERMOPANORPA INAEQUALIS Tillyard

Plate 2, fig. 2; Plate 4, fig. 1; text fig. 3

*Permopanorpa inaequalis* Tillyard, Amer. Journ. Sci., **11** (62), p. 145, 1926.

*Permopanorpa tenuis* Tillyard, *ibid.*, p. 146.

*Permopanorpa gracilis* Tillyard, *ibid.*, p. 147.

*Permopanorpa dunbari* Tillyard, *ibid.*, p. 149.

*Permopanorpa sellardsi* Tillyard, *ibid.*, p. 150.

*Permopanorpa raymondi* Carpenter, Bull. Mus. Comp. Zoöl., **67** (13), p. 438-439, 1926.

Length of ♀, 4.0 mm.; length of ♂, 5.0 mm.

*Fore wing*.—Length, 4.6-5.4 mm.; greatest width, 1.4-1.6 mm. Sc terminating on the costal margin just a little beyond the middle line of the wing; the anterior branch of Sc is usually reduced so that it has the appearance of a cross-vein, but it may also be quite oblique and relatively long; R straight at the base, curving downward just below

hm, then continuing nearly parallel with the longitudinal axis of the wing; the degree of bend in R is somewhat variable; R1 straight, with 1-4 pterostigmatic veinlets; Rs originating at the lowest point in the bend of R; R2 unbranched, or forked distally; R3 and R4 usually simple, but occasionally forked; R5 with 2-3 branches; Rs furcates shortly after its origin, R4+5 dividing just a little before the division of R2+3; M more or less completely fused with R at the base; M1-4 diverging from M5 distinctly before the origin of Rs; M1+2 diverges from M3+4 just beneath the first division of Rs; M2+3 forks a little apically of the separation of M3 from M4, and M2 forks before M1; the free piece of M5 very slightly curved, and the free portion of Cu1 gently sigmoidal; Cu2 and 1A remote distally, but much converged basally; 1A and 2A quite remote; 2A and 3A roughly sigmoidal in shape.

*Hind wing.*—Length, 4.0-4.2 mm.; greatest width, 1.0-1.2 mm. Sc terminating before the middle of the wing, anterior branch missing; R and R1 shaped as in the fore wing, except that the bend in R takes place much nearer the base and is less pronounced; pterostigma shorter than in the fore wing, and with only two pterostigmatic veinlets; Rs originating much nearer to the base than in the fore wing; branching of Rs similar to that of the fore, except that the division of R2 from R3 invariably takes place much more apically than in the fore wing; Cu1+M5 a very straight vein; free part of Cu1 markedly oblique; Cu2 nearly parallel to Cu1+M5 for its entire length; 1A fused to 2A from the base to near the wing margin, where the two veins diverge as a wide fork. Distribution of cross-veins about as in the fore wing, except that the area between the termination of Sc and the beginning of the pterostigma is strengthened by two strong, oblique cross-veins.

*Holotype.*—No. 5058, Peabody Museum.

The following specimens of this species are in the Harvard collection: No. 3009ab, fore and hind wings and most of body; collector, F. M. Carpenter. No. 3010ab, fore wing, excellent preservation; collector, W. S. Creighton. No. 3011ab, fore and hind wings, and portions of body; collector, J. W. Wilson. No. 3012, complete fore wing; collector, F. M. Carpenter. No. 3013, fore wing, splendid preservation; collector, F. M. Carpenter. No. 3014ab, fore and hind wing and parts of body; collector, F. M. Carpenter. No. 3015ab, hind wing; collector, F. M. Carpenter. No. 3016ab, fore and hind wings and parts of body; collector, F. M. Carpenter. No. 3017, hind wing; collector, J. W. Wilson. No. 3018ab, complete fore wing; collector, F. M. Carpenter. No.

3019ab, fore and hind wings and body; collector, W. S. Creighton. No. 3020ab, fore wing; collector, F. M. Carpenter. No. 3021ab, fore and hind wings; collector, J. W. Wilson. No. 3022ab, fore and hind wings, and body; F. M. Carpenter. No. 3023ab, hind wing; collector, F. M. Carpenter. No. 3024ab, fore wing (poor) and parts of body; collector, F. M. Carpenter. No. 3025ab, portions of wings and body ( $\sigma^7$ ); collector, F. M. Carpenter. No. 3026, fore wing and parts of body; collector, W. S. Creighton. No. 3027ab, fore and hind wings, and portions of body; collector, J. W. Wilson. No. 3028ab, fore wings, and body; collector, J. W. Wilson. No. 3029ab, portions of wings and body; collector, F. M. Carpenter. No. 3030ab, parts of all four wings; collector, W. S. Creighton. No. 3031ab, fore wing and part of body; collector, F. M. Carpenter. No. 3032ab, four wings and body; collector, F. M. Carpenter. No. 3033ab, fore wing; collector, F. M. Carpenter. In Dr. Sellards' collection there is only one specimen, No. 1402, consisting of a fore wing.

This species is one of the most completely known fossil insects, and certainly the best known fossil Mecopteran. It possesses several interesting characteristics which one would hardly expect to find in a Permian scorpion-fly. The antennae, which are preserved in three of the Harvard fossils, are shorter than in any other extinct or recent species. In *Chorista* there are upwards of 50 segments; in *Panorpa* and *Panorpodes*, between 40 and 50; in *Merope*, 27-30; in *Nannochorista*, 22-25; in *Boreus*, 20-24; and in *Bittacus*, 16-20. Obviously, in the more highly specialized genera, as *Nannochorista*, *Bittacus*, and *Boreus*, the number of segments is down in the lower twenties or even less; whereas in the more primitive forms, the tendency is to increase this number from 30 to 50. It is therefore very surprising to find a Lower Permian Mecopteran with only 16 segments, a number which is found only in the highly developed *Bittacidae*. The shape of the antennal segments, however, is much more like that in *Merope* than in the *Bittacidae*. The male genitalia of *P. inaequalis* are perhaps the most surprising feature of all. The external genitalia of the males of the *Panorpidae*, *Choristidae*, and *Nannochoristidae* are in the form of a swollen bulb on the end of the abdomen; in *Merope* they appear as a pair of long narrow claspers; in *Boreus* they are very small and reduced. But in the *Bittacidae*, which are considered to be on a level with the *Boreidae* as the most highly specialized of the recent Mecoptera, the male genitalia consist of several thin, almost membraneous appendages, utterly different from those of the other Mecoptera. It is this type of genitalia that the males of *Permopanorpa* possessed, as

shown in text figure 3, so we are obliged to admit that this Lower Permian genus had essentially the same genital and antennal structure as the most highly specialized of our recent Mecoptera.

The variation in the venation and shape of the wing of *Permopanorpa inaequalis* is interesting, also. In order to determine something of the degree of variation which exists in recent Mecoptera, I examined over 3000 specimens of North American species, which were loaned to me by the Museum of Comparative Zoölogy, the American Museum of Natural History, the National Museum, and other institutions.<sup>1</sup> Certain of the species show a remarkable variation in the form of the branches of Rs, a peculiarity which has also been recorded by Esben-Petersen (1921). It is this same vein, as previously men-

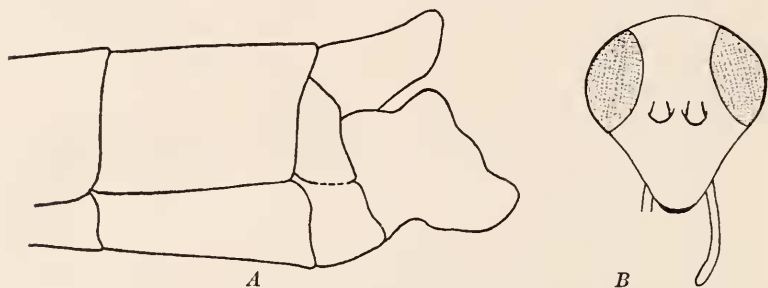


FIG. 3.—*Permopanorpa inaequalis*: A, lateral view of the terminal segments of male abdomen, from specimen No. 3015, M. C. Z.; B, front view of head, from specimen No. 3917, M. C. Z.

tioned, which showed the greatest amount of variation in both *Permopanorpa* and *Platychorista*, so that it seems that at least some of the recent Mecoptera have retained the instability in the structure of the radial sector which was even more evident in the Permian forms. The shape of the wings in most of the species of *Panorpa* shows very nearly as much variation as appears to have been common in the Permian types.

#### PERMOPANORPA FORMOSA Tillyard

*Permopanorpa formosa* Tillyard, Amer. Journ. Sci., 11 (62), p. 144.

There are no specimens of this species in the Harvard collection, and there is no necessity to redescribe the species here. It is quite probable that *P. formosa* is the same as *P. inaequalis*, also, for it does

<sup>1</sup> The results of this study are contained in a monograph of the Mecoptera of North America, now nearing completion.

not possess a single venational characteristic which is absent in some specimen of the latter species. The type specimen, however, is distinctly larger than any of those which have been referred to *P. inaequalis*, and since the basal part of the wing is missing, including the free piece of Cul, it seems advisable to leave the specimen in a distinct species until more evidence is found to the contrary.

*Holotype*.—No. 5057, Peabody Museum.

#### PERMOPANORPA SCHUCHERTI Tillyard

*Permopanorpa schucherti* Tillyard, Amer. Journ. Sci., **11** (62), p. 148.

This species is not present in the Harvard collection. Unfortunately, the half of the type specimen which is at the Peabody Museum is the more poorly preserved, for only one or two of the numerous cross-veins figured by Tillyard are visible. As far as this specimen is concerned, the wing is identical with that of *P. inaequalis*. Tillyard's figure shows the wing much broader and shorter than I believe it actually is. The bend in R is more remote from the base of the wing than he has drawn it, and this is also true of the Cu-M Y-vein, which occupies the same position that it does in *inaequalis*. The arms of the "Y" are unequal, not equal as described by Tillyard, and I am convinced that the cross-vein which he has named the humeral is really another one of the cross-veins present in that area, the true hm being more basal. The basal part of the wing seems to be entirely missing, and its extension would give the wing the more slender habitus of *inaequalis*, with which it is probably synonymous.

*Holotype*.—No. 5061a, Peabody Museum; counterpart, No. 5061b, Cawthron Institute.

#### PROTOPANORPA Tillyard

*Protopanorpa* Tillyard, Amer. Journ. Sci., **11** (62), p. 151, 1926.

*Fore wing*.—Rather broad, with a well rounded apex, and a convex anterior margin; costal area somewhat broader than in *Permopanorpa*; Sc forked dichotomously twice, so that it has three terminal branches; R straight, with at least one pterostigmatic veinlet; Rs with 4-5 terminal branches; M with 6-7 branches; M1 unbranched, M2 forked, M3 simple or forked, M4 branched; Cu-M Y-vein with equal arms; cross-veins weakly formed. Hind wing and body unknown.

*Genotype*.—*Protopanorpa permiana* Till.

This genus was erected by Tillyard for two species, the genotype

and *P. pusilla*. As I have already indicated, however, *P. pusilla* is very different from what Tillyard supposed, and belongs to a separate family, described below.

PROTOPANORPA PERMIANA Tillyard

Plate 3, fig 3; Plate 5, fig. 2

*Protopanorpa permiana* Tillyard, Amer. Journ. Sci., 11 (62), p. 152, 1926.

*Fore wing*.—Length, 5.5 mm.; greatest width, 2.0 mm.; distal branch of Sc terminating on the costal margin, at about the basal edge of the pterostigma; first and second branches of Sc oblique; Rs straight at the base, but diverging downward just beyond hm; R1 straight, diverging upward to the pterostigma from the lowest point in the bend of R; R1 with one pterostigmatic veinlet; Rs originating at the lowest point in the bend of R; first fork of Rs remote from the origin of Rs; R2+3 diverging before the pterostigma; R2 forked or simple; R4+5 separating just below the division of R2+3; R4 simple; R5 forked; M1-4 diverging from M5 before the origin of Rs; the fork on M2 is very deep; M3 is unbranched in most specimens, but may be forked slightly; M4 forks very close to the origin of M3; Cu1 slightly curved, its free piece distinctly arched; Cu2 straight, except at the distal part; 1A very close to Cu2 at the base, but remote distally; both 2A and 3A gently sigmoidal.

*Holotype*.—No. 5064 Peabody Museum, counterpart in Cawthron Institute; paratype No. 5065b in Peabody Museum, counterpart in Cawthron Institute. Two well preserved fore wings of this insect are present in the Harvard collection, numbers 3034ab and 3035ab (F. M. Carpenter).

It should be noted that Tillyard's figure of this wing differs from mine in having a slightly concave anterior margin, instead of convex, as I have drawn it. The type specimen, however, does not lie flat on the rock, but is much twisted and folded. The distal part of the wing, which was hidden by a bit of rock when Tillyard described it, is distinctly plaited or creased at the very apex. A careful examination of the wing shows also that R and Sc are plaited across the middle, as though the front margin had been bent inwards, and as a matter of fact, at the point of greatest concavity of the front margin the wing membrane actually overarches R1 from the anterior side. I am convinced therefore that the true shape of the anterior margin of the type wing was convex, as in the two Harvard specimens, which lie flat on the rock. These two specimens differ slightly in venation from each other and from the holotype. Specimen No. 3024ab possesses a small



fork on the end of M3, as shown in the figure, but this is undoubtedly an individual variation like that of some of the specimens of *P. inaequalis*. The structure of Rs in this specimen is just like that of the holotype, but in the other Harvard specimen R2 and R5 are forked, whereas R3 is simple. These are variations which have already been met in *P. inaequalis*, so that to make a new species for every difference in the branching of the sector would be as unjustified here as in *inaequalis*, since the indications are that *P. permiana* possessed as variable a sector as the former species. One of the interesting features of this wing is the double forking of the subcosta. As can easily be seen in the photograph these branches are dichotomous, not pectinate. This is certainly a very primitive character, only a little more specialized than the condition in the new family *Agetopanorpidae*, where the forking is even more pronounced. Both of the subcostal forks in *Protopanorpa* bear well developed macrotrichia.

Tillyard considered *Protopanorpa* to be directly ancestral to the Liassic *Orthophlebiidae*, which, in turn, gave rise to the recent *Panorpidae*. Whether *Protopanorpa* actually was ancestral to the orthophlebiids is a question which I do not believe can be answered until further details are known about this Permian genus, especially the venation of the hind wing.

#### PROTOCHORISTA Tillyard

*Protochorista* Tillyard, Amer. Journ. Sci., **11** (62), p. 140.

*Hind wing*.—Anterior margin slightly convex, nearly straight; apex well rounded; costal space broad; Sc forked distally; pterostigma well developed, with one veinlet; Rs originating close to the base of the wing; Rs and M with 5 branches; M1, M3, and M4 unbranched; M2 forked. Cross-veins very weakly developed.

*Genotype*.—*Protochorista tetracлада* Till.

This genus was established by Tillyard for two specimens which he placed in different species, *P. tetracлада*, and *P. pentacлада*. After comparison of the types of these two species, I am convinced that they are synonymous.

#### PROTOCHORISTA TETRACLADA Tillyard

##### Plate 5, fig. 1

*Protochorista tetracлада* Tillyard, Amer. Journ. Sci., **11** (62), p. 141.

*Protochorista pentacлада* Tillyard, Amer. Journ. Sci., **11** (62), p. 141.

*Hind wing*.—Length, 5.0 mm.; greatest width, 1.2 mm.; Sc terminating close to the base of the pterostigma; first branch of Sc oblique and

well developed; R with an abrupt bend at the base, just below hm; Rs originating distally of the lowest point in the bend; R1 straight; R2+3 diverging from R4+5 well beyond the origin of Rs; R2 unbranched; R3 forked or simple; R4 unbranched; R5 forked or simple; M uniting with Cu1+M5 before it joins with R; first division of M basally of that of Rs; M1 diverges from M2 distad of the separation of M3 and M4; Cu1 and Cu2 straight, a marked indentation at the termination of Cu2. Anal area is not known (in the figure the anal area of *P. inaequalis* has been sketched in to give some idea of the shape of the wing).

*Holotype*.—No. 5050, Peabody Museum. One specimen in the Harvard collection, No. 3036ab, is a well preserved wing, with the anal area missing.

Both of the specimens in the Yale collection are on a rough surface of the rock, and are consequently more or less distorted. Since the Harvard fossil lies quite flat and has no signs of distortion, it undoubtedly shows the true shape of the wing. I have examined the Yale specimens with much care, but cannot agree with Tillyard on several points. In specimen number 5055 the subcosta is distinctly forked, and terminates on the costal margin; R1 has an oblique pterostigmatic veinlet; R3 possesses a small terminal fork near the margin of the wing (the presence of this fork was ascertained by removing the piece of limestone which covered that part of the wing when Tillyard described it); there is absolutely no sign of the free piece of Cu1 which Tillyard has shown in his figure; and Cu1+M5 joins directly to the base of M. The wing is therefore identical with the one in the Harvard collection, with the exception of slight differences in the branching of the radial sector. The other Yale specimen, No. 5056 has a forked subcosta also, but just before this vein terminates on the costal margin it bends downward and touches R1, as shown in Tillyard's figure. This feature, however, can hardly be of specific importance, since in about 30% of the North American specimens of *Panorpa*, regardless of species, this same peculiarity can be found! In his figure of this specimen, Tillyard has shown more correctly the way in which Cu1+M5 joins the stem of M, although he has indicated the free piece of Cu1 by a dotted line. The specimen is consequently identical with the preceding, except for slight differences in the depth and arrangement of the forks on Rs. Since I have previously shown that Rs is an unstable vein in the other Permian Mecoptera, we are not justified in regarding *P. tetraclada* and *P. pentaclada* as distinct.

That all three of these specimens are hind wings is obvious at once

from the absence of the free piece of Cu1, and the characteristic manner in which Cu1+M5 joins to M. This is also shown by the short, abrupt bend in R and the origin of Rs close to the base of the wing. It seems strange that the hind wings of this species have been found without the fore wing, and one is naturally tempted to believe that the fore wing has been described as a separated genus. The only fore wing which might be thus connected is *Protopanorpa permiana*. This occurs at about the same frequency as *Protochorista*, and the two wings are about the proper size and shape; but in all known specimens of the former species M4 is deeply forked, whereas it is always simple in *Protochorista*. Regardless of this difference, however, I believe that these two species will become synonymous when a complete specimen of one of them has been found.

#### ANORMOCHORISTIDAE

This family was erected by Tillyard for a single wing, *Anormochorista oligoclada* Till., which is not represented in the Harvard collection. Although my examination of the type (No. 5068) convinces me that the peculiar shape of the hind margin is due to a fold in that part of the wing, the venation is so aberrant that the insect obviously had no place in the evolution of recent Mecoptera.

#### LITHOPANORPIDAE, new family

Minute insects, allied to the *Permopanorpidae*.

*Fore wing*.—Shape much as in *Permopanorpa*, costal space narrow; hm present; pterostigma well developed; R1 strongly formed, with several pterostigmatic veinlets; Rs with 4 branches, M with 6; Cu1+M5 well developed, unbranched; Cu-M Y-vein not perfectly formed, M5 being entirely absent as a free vein; Cu1 diverging from Cu2 at the very base of the wing, the free piece of Cu1 being extraordinarily long; Cu2 fused with 1A basally; 3 anal veins present; cross-veins few.

This family is the most highly specialized of any of the Permian Mecoptera yet known. The complete absence of the free part of M5 is a peculiarity found only in the highly developed recent forms, and the long free piece of Cu1 is not present in any known Mecopteran, fossil or recent.

#### LITHOPANORPA, new genus

*Fore wing*.—Slender, rounded apically; anterior margin straight; Sc terminating on the costal margin well before the pterostigma, its

anterior distal branch reduced to a short veinlet; R1 straight, with 2 pterostigmatic veinlets; pterostigma elongate; M1 and M3 branched; M2 and M4 forked; basal part of M (between R and the union of M with Cu1) quite straight, appearing as a basal continuation of Cu1 + M5.

*Genotype*.—*Protopanorpa pusilla* Till.

#### LITHOPANORPA PUSILLA (Tillyard)

Plate 2, fig. 4; Plate 5, fig. 3

*Protopanorpa pusilla* Tillyard, Amer. Journ. Sci., 11 (62), p. 153.

*Fore wing*.—Length, 4.0 mm.; greatest width, 1.3 mm. Sc terminating at about the middle of the anterior margin; R straight at base, but curving gently downward just below hm; Rs originating at the lowest point in the bend of R, just beneath Sc1; first fork of Rs below the termination of Sc; R2+3 dividing close to the margin of the wing, the fork of R4+5 being much deeper; M makes a sharp bend at its junction with Cu1, so that the rest of the stem of the media seems to be a continuation of the free part of Cu1; first obvious fork of M distad of the origin of Rs; M1 diverges from M2 just below the basal part of the pterostigma; M3 separates from M4 basad of the first furcation of Rs; Cu1+M5 gently curved; Cu2 a straight vein; 1A fused with Cu2 for about half its length; 2A terminating on the hind margin, but linked with 1A distally by a strong cross-vein. Other cross-veins weakly formed.

*Holotype*.—No. 5066a, Peabody Museum; counterpart in Cawthron Institute.

When Tillyard described this specimen, the basal two-thirds of the wing was covered up by a fragment of limestone, although Tillyard was under the impression that this portion of the wing was obliterated by a fracture. With Dr. Dunbar's permission, I removed the small chip of rock, exposing the basal third of the specimen, which was utterly different from what Tillyard had assumed. The absence of M5 and the fusion of Cu2 and 1A are suggestive of a hind wing, since the former is a condition found in the hind wings of all known Mecoptera, and the latter, one that is constant in the hind wings of recent Mecoptera. But in all known hind wings of the Permian species (*Protochorista*, *Permopanorpa*, *Platychorista*) there are two constant features: the short bend in R at the base, and the basal origin of Rs. It will be seen in the photograph of *L. pusilla* that the bend in R and the origin of

Rs is precisely like those in the fore wing of the Permian forms, and not at all like the hind wing. Furthermore, the free part of Cu1 is very short and weakly developed in the hind wings, but in *L. pusilla* it is extraordinarily long and well developed. All things considered, it seems certain enough that the holotype of this species is a fore wing.

#### AGETOPANORPIDAE, new family

Small insects, remotely related to the *Permopanorpidae*.

*Fore wing* (?).— Broad, with a rounded apex; costal space very wide, but without the numerous veinlets of *Platychorista*; Sc remote from the costal margin, with several dichotomous forks; hm present; R well developed; R1 slightly undulated; pterostigma very weakly formed; Rs with 4-6 branches; M with 6 branches; Cu-M Y-vein well formed in some species, but incomplete in others; 2 anal veins present.

Within this family I place *Petromantis* Handl. and *Kamopanorpa* Mart., both from the Russian Permian, and the new genus, *Agetopanorpa*, from the Kansan beds. *Petromantis* was originally placed by Handlirsch in the family *Paleomantidae*, as a Permian orthopteran allied to the recent mantids. Martynov, however, having many additional specimens of related forms, recognized the group as mecopterous, and placed this genus and *Kamopanorpa* in the family *Permopanorpidae*. That these genera cannot be assigned to that family is evident from the very broad costal space, the deep branches of Sc, and the very different shape of the wing.

#### AGETOPANORPA, new genus

*Fore wing* (?).— More or less oval, costal margin distinctly arched; distal branch of Sc terminating just before the pterostigmatic area; R parallel with Sc at base, but bending abruptly away just beyond hm.; pterostigmatic veinlets absent, Rs with 5 branches, R5 being forked; M1 and M3 unbranched; M2 and M4 forked; free piece of Cu1 absent, or at least strongly formed; Cu2 remote from Cu1+M5 at base; 1A and 2A free; cross-veins very weakly developed.

*Genotype*.—*Agetopanorpa maculata*, new species.

*Fore wing* (?).— Length, 9.0 mm.; greatest width, 4.0 mm. Costal space narrowed at base; Sc2 longer than Sc1; R1 diverging from Rs just below the first fork of Sc; first fork of Rs well beyond the second fork of Sc; R2+3 and R4+5 divide shortly after their origin and at

about the same level; the fork of R5 is rather deep; M1-4 diverging from Cu1 basally of the origin of Rs; first apparent fork on M just a little before the first fork in Rs; M1 about as long as M3; fork on M2 shorter than that on M4; Cu1+M5 very slightly sigmoidal; Cu2 curved at its ends, but straight for most of its length; 1A fused with Cu2 at the very base; hind margin of the wing with a distinct indentation at the termination of Cu2. The entire wing is covered with irregular brown pigment spots, somewhat larger and more diffuse apically.

*Holotype*.—No. 3037ab, Museum of Comparative Zoölogy; collector, J. W. Wilson.

This wing, although magnificently preserved, is one of the most puzzling of any of the Permian Mecoptera. That it is a Mecopteran is unquestionable; the structure of R1, the radial sector, and particularly the media, which is identical with that of *Protopanorpa*, place it definitely within the order. But the complete absence of the free piece of Cu1 at the base of the wing is a character which has not been found in any other Mecopteran, fossil or recent. The veins stand out with striking clearness and are marked with the large bases of the macrotrichia, so characteristic of the ancient Mecoptera (see photograph, Plate 2, fig. 1). That the free piece of Cu1 could have been present in this wing, yet not preserved, seems to be utterly impossible. Nevertheless, Cu1 does actually make up a major part of the vein labeled Cu1+M5 in the figure, as shown by the convexity and concavity of the veins. M5, alone, would be a weak, concave vein, but in the fossil Cu1+M5 is a strong, convex vein as in all other Mecoptera. We are therefore forced to the conclusion that the free part of Cu1, which ordinarily forms the lower arm of the "Y", has been lost in *Agetopanorpa*. Only one of the Mecoptera of the Russian Permian, *Petromantis kamensis*, Mart., is completely enough preserved to show the base of the wing, and this was described by Martynov as having the Cu-M Y-vein completely formed. The absence of the free part of Cu1 in *Agetopanorpa* is therefore even more perplexing, for in other respects these two wings are identical, in size, shape, and venation, except for the fork of R5 in the Russian form. In view of the phylogenetic significance of the Cu-M Y-vein in the Mecoptera, one would be justified in establishing a separate family for *Petromantis*, if it were not for this startling similarity between it and *Agetopanorpa*. It is hardly conceivable that these two wings can be so much alike in other respects, and yet belong to distinct families. There is, of course, the possibility that *A. maculata* is a hind wing, and *P. kamensis*,

a fore wing. But as I have pointed out in the case of previous species, the origin of Rs in the hind wing is much closer to the base than it is in the fore wing, and in *A. maculata* Rs originates in a manner quite characteristic of a fore wing, and just as it does in *Petromantis*. The explanation of the structure of the cubitus of *Agetopanorpa* will probably become clear enough when additional material has been found, and until then it hardly seems necessary to establish a new family for the Russian form.

There is one other feature of this wing that is peculiar. The vein labeled Cu2, which is distinctly concave, is entirely without the macrotrichia so prominent on the other veins (this absence of macrotrichia can be noted in the photograph). At first I suspected that this apparent vein was only a fold in the wing, but since the next anal vein in the wing is strongly *convex*, and hence must be 1A, the concave vein between 1A and Cu1 must be Cu2. One would naturally suppose that since the macrotrichial bases and color markings are so clear all over the wing, the cross-veins would also be evident; but not one, except hm, is discernible. A wing of this size and shape, however, would be exceedingly flimsy without cross supports, and we must assume that some cross-veins were there, although poorly developed.

The systematic position of *Agetopanorpa* is very obscure. The broad costal area, the well developed branches on Sc, and the 6-branched media, are all primitive characters; in fact, the structure of Sc is probably more primitive than that of any other known Mecopteran. But the loss of the basal piece of Cu1 is a high specialization which eliminates the genus from the line of ancestry of our recent forms, and we must conclude that *Agetopanorpa* represents a well developed end branch of some primitive Mecopteran not known to us at present. It seems probable that the *Agetopanorpidae* was a very ancient family, which also existed during the earlier Permian, or perhaps the Upper Carboniferous, and that *Agetopanorpa* was a Permian survival that had reached a high stage of development along certain lines. The relatively high degree of specialization which some of the Lower Permian Mecoptera seemed to have attained is conclusive proof that this order had been in existence for a long time previous to the Wellington age. But whether these insects arose in the earliest Permian or in the Upper Carboniferous, as Tillyard claims, is a question which cannot be answered with any certainty until more has been learned of the fauna of the Pennsylvanian.

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